# Species patterns: **Evolution's competitive edge**

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**Phylogenetic analyses of island lizard faunas suggest that patterns in species distributions and body size evolution are the result of resource competition.**

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Two scenarios involving competition for limiting resources are often proposed to explain why closely related species differ in size when they occur together. The first, character displacement, involves two species of similar size invading the same area, leading to the evolution of niche displacement and consequent size divergence of the two species. The second explanation, size assortment, involves cases where competitive exclusion prevents species of similar size from colonizing the same area, so that only species that are already sufficiently dissimilar in size can coexist. With character displacement, the size difference evolved within the area being studied, but with size assortment the size difference evolved elsewhere.

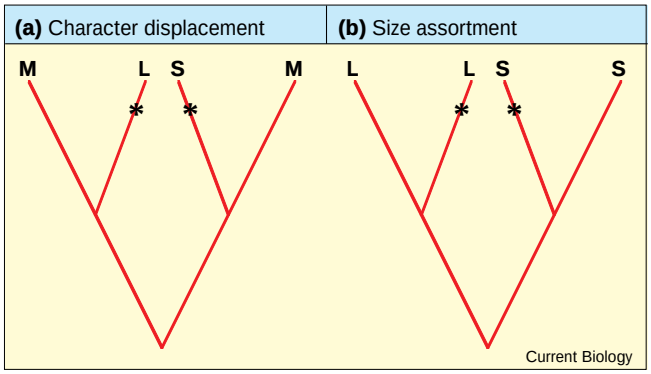
To distinguish between cases of character displacement and size assortment we should, ideally, have a record of the past history of the populations being studied. Phylogenetic information can provide a powerful tool for inferring historical patterns of size change, especially if the likely colonization routes for each species in the study system are known (Figure 1). Working with the Anolis lizards of the Lesser Antilles, and using this phylogenetic approach, Losos [1] identified the branches on the Anolis phylogenetic tree where evolutionary size changes seemed to have occurred, and then asked whether character displacement or size assortment was most likely to have produced the observed patterns of size distribution.

Character displacement would be expected to produce a pattern in which those branches where size change had occurred were the ones where species of different size had come into contact. To test for size assortment, the observed distributions of cases of differential colonization were compared with those expected under a null model of no size assortment. Character displacement was at best a rare occurrence among Anolis species of the Lesser Antilles: large and small species form separate phylogenetic lineages, and changes in body size have therefore rarely evolved. In contrast, a null model of no size assortment was rejected. Losos [1] therefore concluded that size assortment by competitive exclusion was largely responsible for producing the dissimilarity in body sizes of coexisting species.

Radtkey *et al.* [2] have followed the path laid down by Losos, using a system where size change seems to have evolved more frequently. *Cnemidophorous* are diurnal, insectivorous whiptail lizards that occur on the islands in the Sea of Cortez and on the surrounding mainland (Figure 2). These lizard species demonstrate a pattern of morphological variation suggestive of character displacement. On the Baja Peninsula, two species are present, one large (*C. tigris*) and one small (*C. hyperythrus*). Each oceanic island in the Sea of Cortez contains one of the two species, and here they show body sizes intermediate to the species found on the Baja Peninsula. In contrast, land-bridge islands — those on the continental shelf which were at some point connected to the mainland — in the Sea of Cortez contain either one species (usually *C. tigris*) or two species (large *C. tigris* and small *C. hyperythrus*). On mainland Mexico, *C. hyperythrus* is absent and *C. tigris* assumes the role of the smaller species in whiptail guilds.

There is a problem, however, with inferring character displacement in this system, because there are two sources for island colonization by *C. tigris* — from mainland Mexico, where *C. tigris* is medium-sized, and from Baja California, where *C. tigris* is large. It could be that single-species island populations of *C. tigris*, which are all intermediate in size, are all descended from a Mexican colonist, whereas all two-species islands, with small

**Figure 1**




Phylogenies showing the imprints of (a) character displacement and (b) size assortment. An asterisk indicates coinvasion of an island. L, large-bodied species; M, medium-bodied species; S, small-bodied species.

**Figure 2**


Map showing the locations of *C. hyperythrus* and *C. tigris*, on the mainland, and the distribution of species on both oceanic and land-bridge islands in the Sea of Cortez. (Modified from [2].)

*C. hyperythrus*, have *C. tigris* populations that originated from Baja California.

To address this problem, Radtkey *et al.* [2] reconstructed a phylogeny for whiptail lizards using the nucleotide sequences of the cytochrome *b* gene, and from this inferred the evolutionary history of body size changes and the historical patterns of colonization. Ancestral body sizes were reconstructed by taking present-day body size and optimizing it as a continuous character along the most parsimonious phylogeny. This method of optimization allows changes to be inferred on very few or single branches. Thus, examples of character displacement could be easily identified because, once the competitive environment has changed, the imprint of character displacement will occur as a single change along a branch on the phylogeny.

Radtkey *et al.* [2] also constructed a null model to test whether inferred morphological changes were statistically valid, and whether they were in fact caused by, and occurred in the direction predicted by, a change in the competitive environment. Independent contrast values were also calculated using the inferred ancestral body sizes. As species are part of a hierarchically structured phylogeny, they cannot, for statistical purposes, be regarded as independent. For example, closely related species will be more similar by common descent than more distantly related species. The calculation of independent contrast values deals with this problem by estimating differences between pairs of species or other taxa that shared a most common recent ancestor. Each such contrast will have evolved independently of every other contrast [3].

The independent contrast values were then compared under the null expectation that no difference exists along those branches of the phylogeny experiencing a change in the competitive environment, relative to those experiencing no such change. In fact, all the values were found to be significantly different, showing that changes in body size did seem to occur in response to a change in the competitive environment. Changes in the competitive environment were then mapped onto the phylogeny, and a comparison was made between those that occurred in the direction of the predictions of character displacement versus those that did not.

What role did character displacement play in the evolution of body sizes in *Cnemidophorous*? Five out of eight changes in the competitive environment led to an inferred change in body size consistent with the predictions of character displacement. In the remaining three cases, no change in body size occurred. In a further three cases, body size changed in the absence of a change in the competitive environment, but was still consistent with the most recent change in competitive environment. No changes in body size occurred in the direction opposite to that predicted by character displacement.

The role of size assortment was assessed by focusing on those populations where no change in body size had occurred since colonization. The size assortment hypothesis would simply seem to predict that intermediate size *C. tigris* should not occur on two-species islands. However, Radtkey *et al.* [2] also believe that it makes the prediction, which we believe might be questioned, that large *C. tigris* should occur only on two-species islands. A measure of the role of size assortment in shaping body size distributions is given by comparing the number of taxa that conform to this expectation relative to the number that violate it. This analysis was performed for single-species oceanic islands and for both single-species and two-species land-bridge islands, because size assortment, unlike character displacement, can occur over ecological, not just evolutionary, time.

It turned out that populations on four out of seven single-species oceanic islands have body sizes that are consistent

with the predictions of size assortment. All two-species land-bridge islands are also consistent, whereas all single-species land-bridge islands are inconsistent with the predictions of size assortment. From their analysis, Radtkey *et al.* [2] concluded that character displacement and size assortment have both contributed to much of the observed variation in body size of *Cnemidophorous* lizards on the islands of the Sea of Cortez and the surrounding mainland. Ecological displacement resulting from resource competition therefore seems to have moulded body size and species distributions throughout the region.

By incorporating phylogenetic methods into community ecology, Radtkey *et al.* [2] have developed the fruitful approach pioneered by Losos, but the *Cnemidophorous* system now needs experimental work. If body size differences are in fact adaptations that allow optimal resource utilization, experimental manipulations will be required to show that fitness is dependent on the abundance and frequency of differently sized competitors. Luckily, Nature often provides help for the experimental evolutionary biologist. In this case, it may well be possible to introduce a second species to the single-species land-bridge islands in the Sea of Cortez, and then to test for divergent natural selection in the populations.

As Radtkey *et al.* [2] have so elegantly shown, a combination of phylogenetic and biogeographical data can usefully contribute to the wider debate concerning the role of competition in both structuring ecological communities and dictating evolutionary processes.

## References

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